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A RARE BIPINNATE MICROSPOROPHYLL ATTRIBUTABLE TO THE CYCADALES, FROM THE LATE TRIASSIC CHINLE FORMATION, PETRIFIED FOREST NATIONAL PARK, ARIZONA.

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ABSTRACT ---A single specimen collected in the Petrified Forest National Park, Arizona, from the Upper Triassic Chinle Formation, is the first bipinnate male sporophyll to be attributed to the order Cycadales. The sporophyll has a broad stalk, four sub-opposite pairs of first order pinnae and an apical pinna, all bearing short pinnules around their margins. Cuticle characters include: typically cycadalean epidermal cells; three types of trichomes, un-branched, branched, short conical; a haplocheilic stoma; monosulcate pollen. Putative pollen-sacs are compared with similar features in extant cycads which support the attribution. *Androcycas* gen. nov. is erected to accommodate the microsporangiate sporophyll as *Androcycas santuccii* sp. nov.

Keywords: Triassic, Petrified Forest, Chinle Formation, Cycadales, microsporophyll

INTRODUCTION

CYCADS ARE gymnospermous seed-plants with widespread but disjunct distribution in tropical, sub-tropical and warm temperate climates (see Jones, 2002, p. 8 for map). They are often referred to as 'living fossils' for several good reasons, especially their production of primitive, motile male gametes (multi-flagellated spermatozoa), a feature shared only with *Ginkgo biloba* amongst seed-plants. The Cycadales are of great antiquity, with their origins in the Paleozoic, and are fundamentally little changed since the Mesozoic, having reached the zenith of their evolution by the Jurassic or early Cretaceous (Pant, 1987, 2002). Living cycads were still quite poorly understood when Chamberlain (1919; 1935) undertook his outstanding pioneering work on the group. There are now eleven extant genera recognized including about 290 species placed in three families, the Cycadaceae (with only *Cycas*), Zamiaceae (with *Ceratozamia*, *Chigua*, *Dioon*, *Encephalartos*, *Lepidozamia*, *Macrozamia*, *Microcycas* and *Zamia*) and Stangeriaceae (with *Bowenia* and *Stangeria*) (Hill, 1998-2004; Jones, 2002; Whitelock, 2002).

All cycad species have separate female and male plants (dioecious) with spiral flushes of pinnate foliage-leaves alternating with flushes of scale-leaves around the apex of the stem. The sexes are distinguishable only by their cones with either naked ovules or pollen-sacs. Both sexes of cones are compact and terminal in all cycads except for the female plant of *Cycas* in which leaf-like megasporophylls (Fig. 3.2) are produced in the phyllotactic spiral, forming a pseudocone (Fig. 3.1). In time the apex of the stem continues to grow, reverting to production of foliage and scale leaves until the next reproductive phase (Pant and Mehra, 1962, p. 89).

Figures 1.1 and 1.2 show the part and counterpart respectively of a highly distinctive and unusual, if not unique, pinnate microsporophyll. The gross morphology shows a strong resemblance to megasporophylls of the *Cycas*-type (Fig. 3.2) and the specimen was recently figured (Watson and Cusack 2005, fig. 78E), as the probable sterile distal part of such a megasporophyll. However, subsequent detailed study by light (LM) and scanning electron microscopy (SEM) has unexpectedly shown this suggestion to be incorrect. The new information presented here indicates that the specimen is a bipinnate microsporophyll, bearing monosulcate pollen along with other cycadalean features. Pinnate cycad megasporophylls are quite well-known from the fossil record (Watson and Cusack, 2005), but as far as we can ascertain, this is the first evidence of a pinnate male structure attributable to the Cycadales. All other known cycadalean microsporangiate reproductive structures, both fossil and extant, including those of *Cycas*, are compact cones with blade-like microsporophylls bearing pollen-sacs on the abaxial surface (Norstog and Nicholls, 1997: 71). Male cones of extant cycads are extensively illustrated by Jones (2002), Whitelock (2002), and Hill (1998-2004). Fossil male cones of putative cycadalean affinity have been described from the Permian onwards (Zhu and Du, 1981) but reports are few in number compared with records for female structures (Pant, 1987; Gao and Thomas, 1989; Norstog and Nicholls, 1997; Jones, 2002). Most recently, Klavins et al. (2003) have presented a detailed study of a cycad male cone, from the Middle Triassic of Antarctica, which is the first record of a microsporangiate cone with internal anatomy preserved.

Because the new Upper Triassic specimen presented here resembles none of the cones, of any age, hitherto described, it is necessary to erect a new genus, in which to accommodate it as a new species.

MATERIAL

The new taxon is known only from a single specimen split into part (PEFO 34158; Fig. 1.1) and counterpart (PEFO

34158A; Fig. 1.2), deposited in the collections at Petrified Forest National Park, Arizona. The specimen was collected across the main park road about 300 meters east of the small hills called The Tepees in the central part of the Petrified Forest. The site has been assigned locality number PFP 004 in the collection records of Petrified Forest National Park. Qualified investigators may obtain its exact location from the Chief of Resource Management, Petrified Forest National Park.

The horizon is in a bed, about 20 meters thick, of greenish-grey, generally massive structureless mudstone in what is currently called the Newspaper Rock bed of the Blue Mesa Member of the Late Triassic Chinle Formation (Parker, this volume). The mudstone unit in the Newspaper Rock bed which contained the fossil has been the source of most of the foliar and cone material previously described from the Park (Ash, 1987). For many years the mudstone unit was included in the lower part of the Petrified Forest Member of the Chinle Formation and later assigned to the Monitor Butte Member (Demko et al., 1998). More recently it has been referred to the Blue Mesa Member (Woody, 2003; this volume). Demko (1995) has suggested that the mudstone unit was deposited in an overbank wetland area adjacent to the high-sinuosity channel in which the sandstone facies of the Newspaper Rock bed was deposited.

METHODS

The macro-photographs in Fig. 1 were taken using a Canon 20D digital camera, with the specimen fully immersed in colourless paraffin (kerosene) in order to increase the contrast between the sample and the matrix. This produced results superior to the use of cross-polarised light on a dry specimen. The photo-micrographs were taken using the same camera attached to a Leitz Dialux microscope and the scanning electron micrographs were recorded digitally using a Jeol SEM.

Specimen PEFO 34158 is preserved as a compression with its inner tissues densely coalified and strongly resistant to oxidative maceration by conventional techniques. The necessary extended use of Schulze's solution, combined with the cleated nature of the carbonaceous material, causes the cuticle to disintegrate and dissolve and fails to yield usable preparations. However, with the use of modified techniques (Watson and Cusack, 2005) it has been possible to obtain and figure both SEM mounts and LM slides, regrettably with lack of clarity regarding their original, precise position on the hand specimen.

SEM preparations for studying surface features were obtained by a simple technique using nail varnish painted over the area to be sampled. This efficiently holds the cleats together, during mechanical removal and the subsequent dissolving of attached matrix in hydrofluoric acid. The resulting cleaned, un-macerated sample is then attached to a stub using double-sided tape (for permanent mounting) or nail varnish if the sample is to be removed (with acetone) and turned over for further study (see Watson and Cusack, 2005 for details). Figs 2.1 and 4.1 show samples prepared by this method and mounted with nail varnish.

Isolated cuticle preparations for light microscopy (Figs 2.3, 2.7, 5.1-4) were much less successful. However, none of the gentler agents, such as sodium hypochlorite or nitric acid alone, was effective in isolating the cuticle and we had to resort to the use of Schulze's solution. Unfortunately, the only surviving pieces of cuticle were minute scraps (Fig. 5) recovered with a one-haired paintbrush for mounting on slides under cover slips.

SYSTEMATIC PALEONTOLOGY

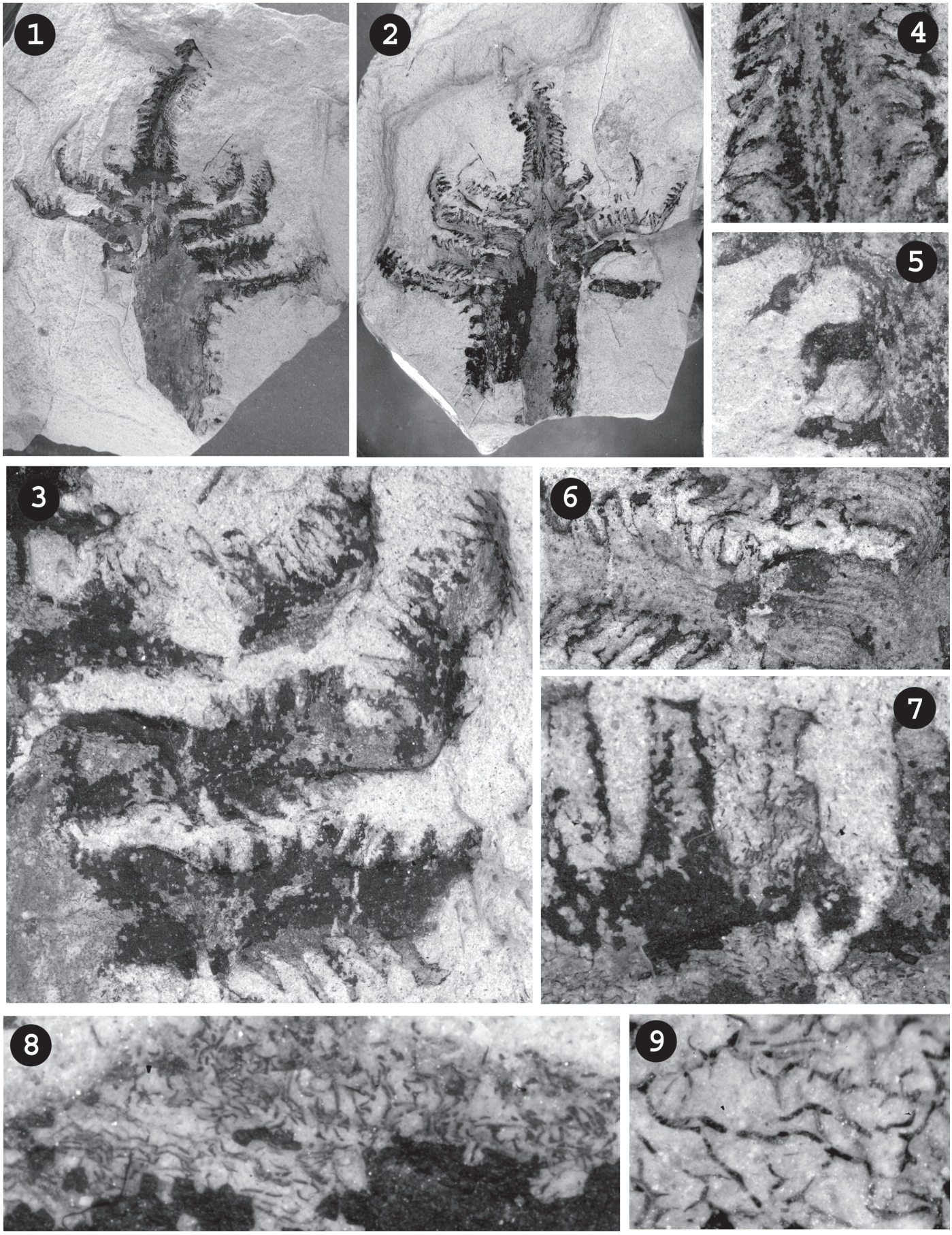
Order CYCADALES
Genus ANDROCYCAS new genus

Diagnosis.–Microsporangiate reproductive organ with pinnate, laminar microsporophylls. Proximal region of sporophyll forming flat, wide stalk; lamina widening distally, divided into lateral and apical pinnae bearing pollen-sacs containing monosulcate pollen.

Etymology.– The Greek andros (male) and the Greek cycas were combined to form a name that emphasizes the similarity of the fossil to the living cycad genus *Cycas*.

Discussion.–The few genera available for fossil cycad male cones all refer to compact cones or simple sporophylls, with various different pollen types (van Konijnenburg-van Cittert, 1971). *Androstrobus* Schimper (1870), the genus most commonly used for Mesozoic male cones (Harris, 1964; Watson and Cusack, 2005), includes species with monosulcate pollen, some clearly bearing a resemblance to extant cycad cones, others poorly distinguished. *Delemaya* Klavins, Taylor, Krings et Taylor (2003), recently established for the structurally preserved type species, *Delamaya*

Figure *1. 1-8*, *Androcycas santuccii* sp. nov. *1*, *2*, holotype at natural size; *1*. half of specimen designated as the part, with abaxial surface attached to matrix, PEFO 34158; *2*. half of specimen designated as the counterpart, with adaxial surface attached to matrix, PEFO 34158A; *3*. Inflected lateral pinnae on right of specimen in Fig. 1.1 showing absence of pinnules basally, x5; *4*. Apical pinna showing backward-pointing pinnules with terminal spines; traces of surface striations visible along left- hand pinnules, x5; *5*. Spinose pinnules from proximal margin, where sporophyll widens to left (see Fig. 1.2), x5; *6*. Exposed matrix on surface of counterpart showing adaxial surface ridges and grooves, x5; *7*. Close-up view of pinnules with terminal spines visible, x15; *8*. Exposed matrix on surface of part showing numerous detached hairs from the tomentose abaxial surface, x30; *9*. Close-up showing several branched hairs amongst the majority of un-branched hairs, x60.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spinulosa Klavins et al. 2003, comprises more or less scale-like sporophylls, helically arranged around a cone axis. Neither of these, nor any other established genus, can accommodate the Chinle specimen described here.

We have thus erected *Androcycas* gen. nov. with a minimal diagnosis, which will allow it, should the need arise, to be adopted for usage in the cautious style of the late Sir Albert Charles Seward (1917) and the late Tom Harris (1961, 1964), which more or less equates to the old paleobotanical use of the organ-genus. Whatever the phylogenetic objections to this sparse approach, it continues to be indispensable for problematical (particularly fragmentary) material (Watson et al., 1999); particularly in offering respite from the proliferation of new genera based on thin evidence.

ANDROCYCAS SANTUCCII new species
Figs. 1, 2, 4-6.

'probable cycad megasporophyll' Watson and Cusack, 2005, p. 126, fig. 78E.

Diagnosis.–Sporophyll at least 8cm long; spreading to at least 7cm wide. Stalk about 2cm wide, parallel-sided, bearing lateral, marginal pinnules typically 2-3mm long and 1.5mm wide, each with 1 or 2 distal spines; sporophyll widening abruptly, approximately half way along length; distal region pinnate, divided into sub-opposite, pinnulate segments, 4-5 attached laterally on each side, single tapering pinna forming apex. Pinnae inflexed; lacking pinnules in basal quarter; pinnules present beyond, spaced 1-1.5mm apart, typically 2-3mm long and 1.5mm wide, with pointed, blunt or square apex bearing 1 or 2 pointed spines. Adaxial surface of sporophyll ridged longitudinally, density of ridges on stalk, about 1.5-2.5 per mm; ridges curving onto surface of pinnae and onto pinnules to form 1-3 fine striations present to pinnule apices. Abaxial surface densely tomentose, trichomes of un-branched and branched types, lengths up to at least 300µm. Cuticle [origin undetermined] with scattered hair bases and stomata; stomatal apparatus haplocheilic; guard cells exposed at surface, surrounded by 6 or 7 unspecialized, straight-walled, subsidiary cells; ordinary epidermal cells in ill-defined, short files, shape square, rectangular or with oblique end walls; cuticle of anticlinal walls of irregular thickness with slightly beaded appearance. Pollen grains ellipsoidal, typically 40µm long; proximal face and sulcus smooth; distal surface finely granulate.

Etymology.–*Androcycas santuccii* sp. nov. is named in honor of Vince Santucci, formerly park paleontologist at the Petrified Forest National Park, who recognised the importance of this unique specimen and drew it to the attention of the junior author.

Holotype.–Specimen PEFO 34158 (part, Fig. 1.1) and PEFO 34158A (counterpart, Fig. 1.2), deposited in the collections at Petrified Forest National Park, Arizona.

DESCRIPTION

General morphology.–The leaf-like nature of *Androcycas santuccii* sp. nov. is evident in Fig. 1.1, 1.2, with four main pairs of sub-opposite, first order pinnae forming the expanded distal region between the tapering apical pinna and the narrower, proximal region which forms a wide, flat, parallel-sided stalk. Unfortunately, the basal part of the stalk, which must include the area of attachment, is not preserved. Small pinnules, 2-3 mm long and about 1.5 mm wide, present along one margin of the stalk (Fig. 1.2), are enlarged in Fig. 1.5 to show their apical spines. They are similar in size and shape to the second order pinnules which form most of the margins of the main pinna segments (Fig. 1.1-1.4, 1.6, 1.7) but are absent, or poorly developed, in the slightly swollen basal part of the pinna (Fig. 1.3, 1.6). The pinnules appear to be rather variable in shape, some clearly defined, others less well so. Of those presenting good evidence of shape, some appear pointed with a single apical spine (Fig. 1.4, lower left) whilst others are clearly square-ended with two or three terminal spines (Fig. 1.7). Some of the differences are almost certainly preservational effects upon pinnules which are folded or damaged in life. Other damage might be caused by the distinct tendency for the substance of the pinnules to separate into different parts when the specimen was split along the bedding plane. This has resulted in well-defined coaly rims on one surface (Fig. 1.4, 1.6, 1.7) and the central parts of the pinnule on the other (Fig. 1.3).

It is fortuitous that the coalified remains adhere in random patches to one or other of the two halves, thus exposing informative areas of matrix on the corresponding opposite side. It was not immediately obvious how the adaxial and abaxial surfaces could be distinguished and our conclusions are based mainly on the features visible in the exposed matrix, compared to similar features known in other fossil and living cycads. We suggest that the half in Fig. 1.1 (the part) is attached to the matrix by the abaxial surface and that the counterpart (Fig. 1.2) is attached by the adaxial surface.

Adaxial surface.–The exposed matrix of the counterpart (Fig. 1.2) is marked by impressions of a series of grooves and ridges disposed longitudinally along the stalk and central pinnate region. Laterally, they curve outwards and run longitudinally to the apex of each pinna (Fig.1.6), and also curve onto the pinnules (Fig. 1.4) reducing in number to two or three which end at the spinose apex. We are unable to ascertain whether the ridges might relate to compression of veins, or other resistant tissues such as fibres, because the exposed coaly adaxial surface of the part (Fig. 1.1) is singularly uninformative on the

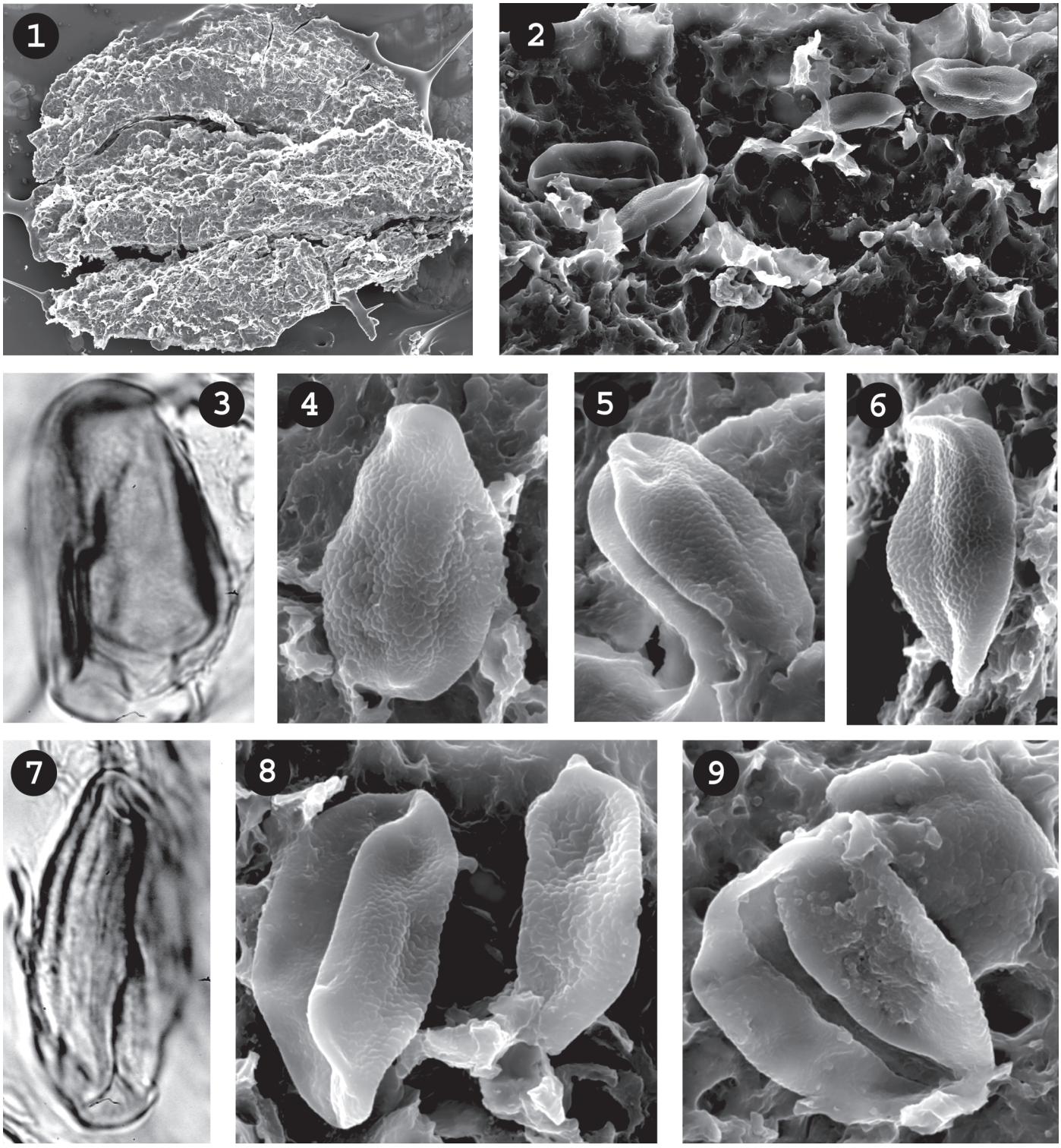

Figure *2. 1-9*, *Androcycas santuccii* sp. nov. *1*. Preparation from basal margin of counterpart showing possible pollen-sacs, x60; *2*. Part of specimen in Fig. 1.1 showing four embedded pollen grains, x500; *3-9*. Pollen grains, all x1500. *3*, *7*. Grains in LM with sulcus and granular sculpture of exine visible; *4-6, 8*. Grains in SEM showing sculpture on distal surface; *9*. Grain with sulcus comparable to *Cycas revoluta* grain in Fig. 3.4.

matter. The petrified male cone *Delemaya spinulosa* Klavins et al. 2003 from the Middle Triassic of Antarctica, also has longitudinal adaxial ridges (Klavins et al., 2003: figs 2A, 4B) which continue onto the prominent apical projections of the scales. There is clearly no connection with either vascular tissue or fibres in *D. spinulosa*. In the light of this similarity it seems likely that the striations of *A. santuccii* are also on the adaxial surface of the sporophyll.

Abaxial surface.–The exposed matrix of the part of *A. santuccii* (Fig. 1.7, 1.8, 1.9) shows masses of detached epidermal hairs separated from the sporophyll surface which is attached to the counterpart. A profuse covering of epidermal

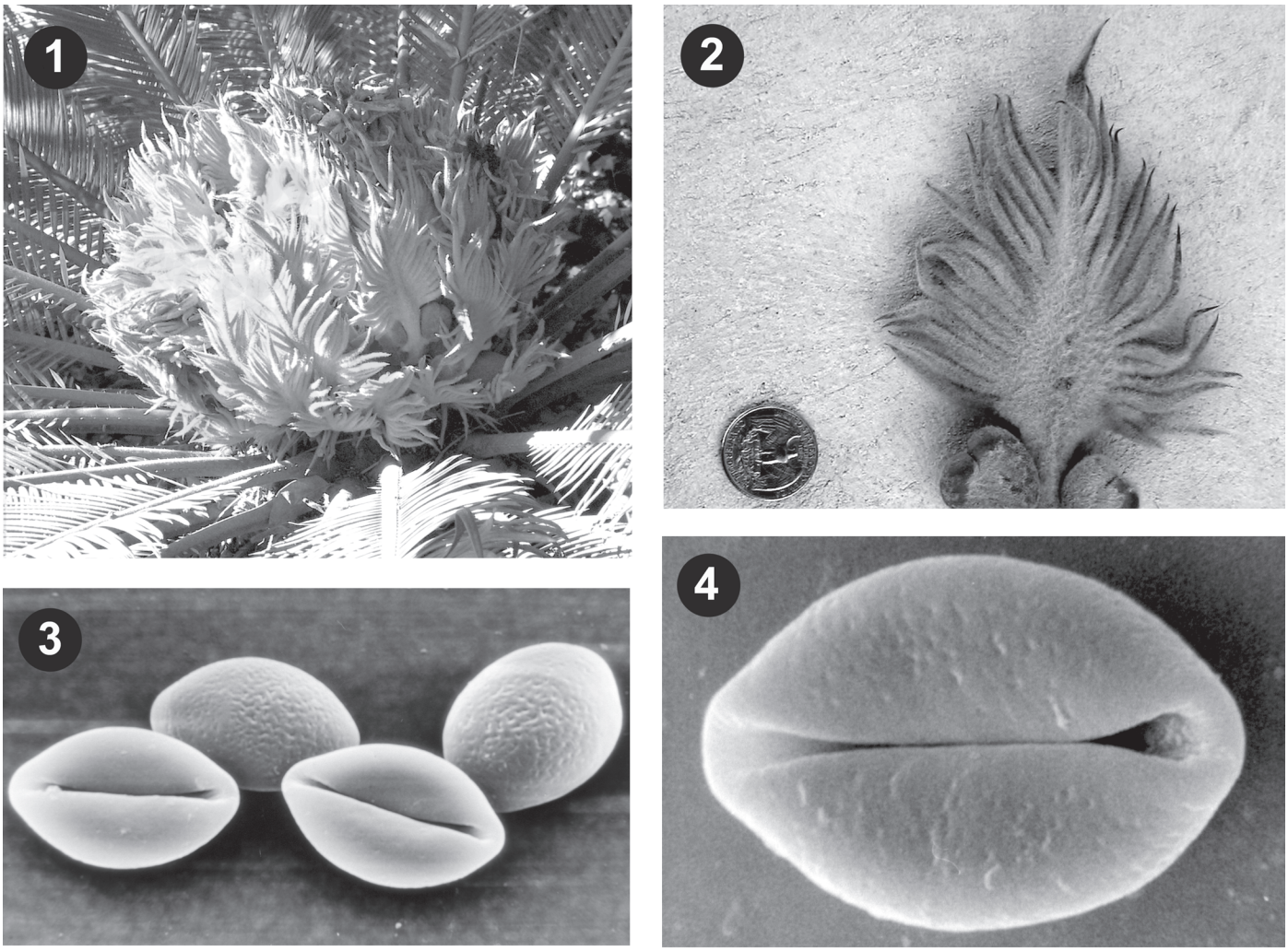

Figure *3. 1-4*, *Cycas revoluta*, living cycad. *1*. Pseudocone on female plant growing at The Mirage Hotel, Las Vegas, showing pinnate megasporophylls; *2*. Megasporophyll from same plant showing densely furry abaxial surface and some individual pinnae inflexed or reflexed; *3*, *4*. Pollen grains from cone of male plant growing in glasshouses at The Firs Botanical Experimental Grounds, University of Manchester; *3*. Grains showing monosulcate proximal face and finely pitted distal surface, x1000; *4*. Grain with sulcus comparable to *Androcycas* fossil grain in Fig. 2.9, x3000.

hairs on young leaves and cones is a common feature of cycads and Figure 3.2 shows the hairs on the abaxial surface of a *Cycas revoluta* megasporophyll. A dense tomentum on the abaxial surface of the microsporophyll is also characteristic of the male cone of some extant cycad species (Pant and Mehra, 1962, p. 79; Watson and Cusack, 2005, fig. 84D, I, J); hence our suggestion that the densely hairy surface of *A. santuccii* is abaxial.

The trichomes in *A. santuccii* are of three types, long un-branched, long branched (seen on the matrix), and short conical (seen on the cuticle). The most prolific are the long un-branched hairs (Figs 1.8; 4.3) with fewer branched hairs amongst them (Fig. 1.9). Detached hairs of *A. santuccii* in the matrix measure up to 300µm in length but this is probably a conservative figure, because the basal portion of most hairs remains attached to the coaly surface. *In situ* hairs and hair bases on the abaxial surface were exposed in an un-macerated SEM preparation (Fig. 4.1) taken from the apical pinna on the part specimen. This coaly piece was detached after it was coated in nail varnish, cleaned in HF and mounted on a stub. In effect this achieves the same result as the classic 'transfer technique' (Walton, 1923; Banks, 1970, p. 10) for turning over plants preserved as compressions, but on a very small scale. The hairs seen in this preparation are only about 50µm, with many of them lacking well-defined tips (Fig. 4.2), though the hair in Fig. 4.3 is an exception, being incomplete at its base. Because the hairy abaxial surface was freed from the matrix by dissolving the latter in HF, we conclude that the long parts of the hairs were detached sometime during the preservation process and not mechanically damaged by splitting after collection. This might be the case with the majority of the hairs visible on the exposed matrix (Fig. 1.8, 1.9). The much shorter hairs in Fig. 5.2 are discussed below.

Pollen-sacs.–In extant cycads the pollen-sacs (microsporangia) are borne abaxially and there is some evidence for a marginal abaxial position in *A. santuccii*. The sample in Fig. 2.1 is one of our un-macerated preparations held together with nail varnish. The obvious division into three appears to us to be

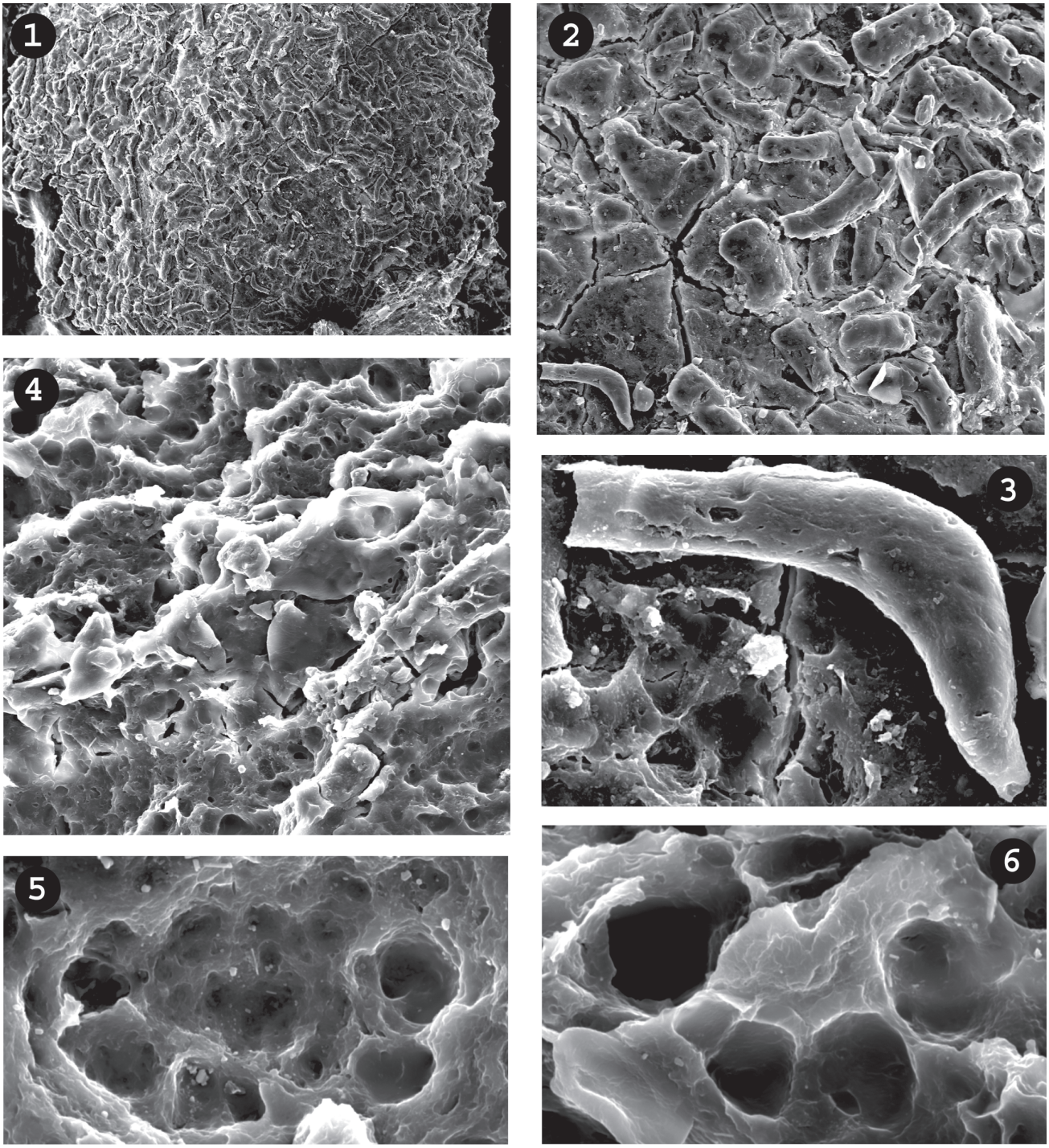

Figure *4. 1-6*, *Androcycas santuccii* sp. nov. *1*. Abaxial surface of scale showing dense covering of epidermal hairs, x100; *2*. Close-up of abaxial surface showing individual hairs and hair bases, x400; *3*. Single un-branched epidermal hair, x2000; *4*. Closer view of un-macerated SEM preparation in Fig. 2.1, possibly showing inside view of pollen-sac; see text for discussion, x400; *5*, *6*. Typical circular groups of cells from same preparation, possibly surrounding basal cell of trichome; group in Fig. 6 can be seen at top left of Fig. 4, x1500.

a natural feature with well-defined edges, rather than cracks or cleats, and we are inclined to suggest that they are the remnants of a trio of disrupted pollen-sacs. The sample was taken as a generous piece from the lower left of the counterpart (Fig. 1.2) and cleaned in HF, in the hope of exposing and investigating the lateral pinnules on the stalk. Most of the coaly sample disintegrated in HF, producing minute fragments of cuticle and unrecognisable debris, leaving the sample in Fig. 2.1 as the only sizeable piece, still attached to the nail varnish. Viewed in the SEM it is immediately clear that the effect of the HF treatment, rather than exposing a clean adaxial surface, has been to produce a view of an internal tissue composed of small cells (Fig. 4.4, 4.5, 4.6), probably with quite thick walls. The coalified nature of this sample prevents a clear view of the cell arrangement, except that in places they

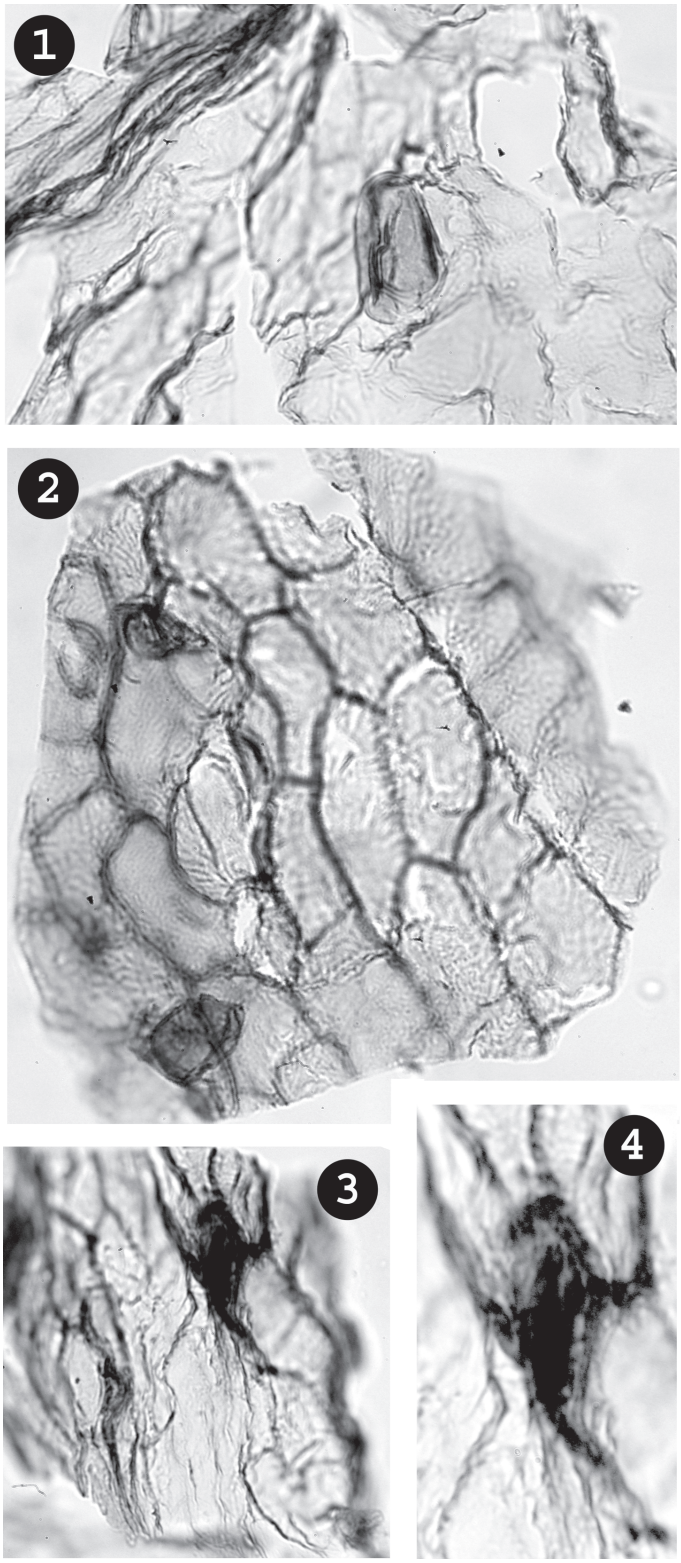

Figure *5. 1-4*, *Androcycas santuccii* sp. nov. *1-4*. Scraps of thin, delicate cuticle in LM, possibly pollen-sac walls. *1*. Cuticle with pollen grain seen in Fig. 2.3, x500; *2*. Largest piece of cuticle isolated showing two hair bases and ordinary epidermal cells of typical cycadalean type, x500; *3*. Scrap of cuticle with one or two stomata present (see also Fig. 6); dark shadow at top left margin is part of the pollen grain seen in Fig. 2.7, x500; *4*. Enlarged and re-focussed stomatal apparatus showing haplocheilic features (see text for discussion), x1000.

are seen to be disposed in rings (Fig. 4.5, 4.6), around an obscure central structure. This is certainly not a stoma and the possibility of it being a trichome base is discussed below.

A striking feature of this preparation is the presence of numerous, scattered, monosulcate pollen grains (Fig. 2.2), some of them quite deeply embedded, presumably present from before the time of the sporophyll's demise. It seems possible, even likely, that these grains are lying amongst the cellular remains of the inner layer of disrupted pollen-sacs. If this is so, it would seem that the microsporangium was a sessile rather than a stalked structure. The group of three side-by-side, putative sacs (Fig. 2.1) is about 1mm across and a little over 1mm long, a size which matches the distal end of pinnules where they might have been located on the abaxial surface.

Pollen grains.–The typically cycadalean ellipsoidal, monosulcate pollen grains (Figs 2.2-2.9; 6) are all obviously similar in original shape, size and exine sculpture, though with differences resulting from the effects of compression. The grain in Fig. 2.9 shows the longitudinal sulcus in an open condition and also displays the lack of sculpture on the proximal face. Many grains are folded along the line of the sulcus, giving a lateral view (Fig. 2.5, 2.6, 2.8) which shows the granular sculpture on the distal surface. Fig. 2.4 shows a grain presenting the full distal face. All the SEM views are of grains attached to the sample in Fig. 2.1. The two grains seen in the LM in Figs 2.3, 2.7; 5.1; 6 are attached to the tiny scraps of thin cuticle described below and match the grains seen in the SEM.

Cuticle and stomata.–Failure to obtain satisfactory cuticle preparations has been the most problematic aspect of this study, with Figs 5 and 6 indicating the continuing lack of success. Three pieces were isolated for study by light microscopy (Fig. 5.1, 5.2, 5.3) each measuring less than 200mm across. They were retrieved with a one-haired paintbrush from the sludgy residue produced in an attempt at a maceration of pinnules from the apical pinna of the counterpart. Unfortunately, the original position on the sporophyll of these pieces of epidermis still remains a matter of conjecture. Nevertheless, the cuticular evidence is sufficient for several features to be picked out as distinctly cycadalean.

The epidermal cells in Fig. 5.2, 5.3, with their variation in shape, oblique end walls, and arrangement in short files, have a typical form which is well-known in many fossil cycads. Two short trichomes are associated with these cells, the upper one apparently intact with a short, pointed apical cell. They are much more widely spaced than the profusion of hairs in the matrix would suggest and this paucity of hair-bases indicates that this cuticle is probably not from the main abaxial lamina of the sporophyll.

The one stomatal apparatus which has been positively identified is seen in Fig. 5.3, 5.4. It is clearly haplocheilic with 5 or 6 unspecialised subsidiary cells, which is typically

cycadalean, but the poorly developed guard cells suggest that it might not have been fully functional. It is probably not from the main surface of the sporophyll.

COMPARISONS

In the absence of any known fossil cone-scales with similar morphology to *A. santuccii* we have indicated the closest comparable features we can find in living cycads. The main sources of detailed information on extant cycad epidermis and cuticle are the works of Pant et al. from the 1960s. Harris (1964) has described several Jurassic male cones with cuticle details. Watson and Cusack (2005) have used LM and SEM illustrations of leaf and cone cuticles for comparisons between Lower Cretaceous and extant cycad species.

Large trichomes.–Epidermal hairs on the leaves of living cycads are known in considerable detail from studies by Stevenson (1981). All have two cells, a basal cell and a longer apical cell (branched or un-branched) and various examples of sporangial hairs have been figured by Pant (2002, pp. 82, 213; repeated from Pant and Nautiyal 1963). The long hairs in the matrix of *A. santuccii* are closely similar to many of these modern examples. Amongst fossil cycads details of hairs are much less well-known, though hair bases are common. *Becklesia anomala*, an English Wealden cycad is unusual in having multicellular trichome bases on the leaves (Watson and Cusack, 2005, figs 8D, 9L, K), with groups of cells which are reminiscent of the circular groups in Fig. 4.5, 4.6. In seeking cuticular features comparable to those of *A. santuccii* we found several closely similar examples in the work of Pant et al. (1962, 1963; Pant, 1973) on recent sporangia. *Dioon edule*, for example, provides three matches.

Sporangial epidermis.–The cycad pollen-sac is often 5-6 layers thick (Pant and Mehra, 1962, p. 82, fig. 40; Pant, 1973, p. 103) with an outermost layer termed the exothecium (= epidermis), a lining called the tapetum, and a middle zone of thin-walled cells sandwiched between them (Pant and Mehra, 1962, p. 81; Pant, 1976, p. 104). The exothecium generally has cells of different size and shape at the apex, middle and base of the sporangium (Pant and Nautiyal, 1963, p. 314, table 10).

The thick-walled cells in Fig. 4.4-4.6 resemble thick-walled exothecium from the sporangium apex of *Dioon edule* (Pant and Nautiyal, 1963, p. 311, fig. 24H) and are also similar to basal sporangial cells of *Microcycas calocoma* (Pant and Nautiyal, 1963, 313, fig.26F). The rings of cells in this layer (Fig. 4.5, 4.6) resemble several examples of prominent hair bases encircled by distinctive cells, given by Pant and Nautiyal (1963), including their text-figs 10B, D (*Encephalartos*) and 21A (*Stangeria*), but these are in leaf epidermis. The central structure in Fig. 4.6 certainly looks very much like a trichome base.

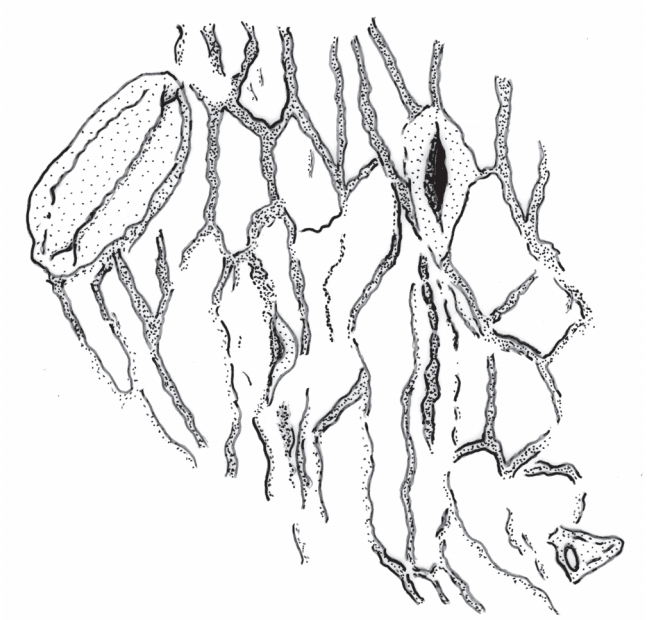

Figure *6. Androcycas santuccii* sp. nov. *Camera lucida* drawing of cuticle in Fig. 5.3, showing a poorly developed stomatal apparatus (top right) clearly of a haplocheilic, cycad-like construction; a possible laterally squashed stoma (approximate center); ordinary epidermal cells of typically cycadalean form; a short, pointed trichome (lower right); monosulcate pollen grain (top left, also seen in Fig.2.7), x1000.

The cells in Fig. 5.2 are of the typical cycad type seen and discussed for many examples of fossil and extant leaves (Pant and Mehra, 1962; Harris, 1964; Pant, 1973; Watson and Cusack, 2005). But in particular they look very similar to cells figured by Pant and Nautiyal (1963, text-fig. 24J) from the middle region of a *Dioon edule* sporangium.

Sporangial trichomes.–The short, pointed trichomes in Fig. 5.2 are similar to short hairs and hair bases figured by Pant and Nautiyal (1962, figs 24H, 25E) on the surface of the microsporangium in *Dioon edule* and *Ceratozamia mexicana*. They also found trichomes on the sporangia of *Encephalartos* sp. and *Zamia floridiana*.

Sporangial stomata.–stomata have been recorded by Pant and Nautiyal (1963) on the sporangium in *Bowenia*, *Ceratozamia*, *Encephalartos*, *Macrozamia*, *Microcycas*, *Stangeria* and *Zamia*, but not in *Cycas* or *Dioon* (Pant and Mehra, 1962, p. 83). A sporangial stoma of *Bowenia serrulata* figured by Pant and Nautiyal (1963, fig. 28B) is closely similar to that of *A. santuccii*, with narrow exposed guard cells and narrow polar subsidiary cells.

In view of the list of similarities to sporangial features in extant species we think that the three cuticle preparations of *A. santuccii* (Fig. 5) are from the outer layer (exothecium) of the exposed wall of a pollen-sac.

Monosulcate pollen.–The pollen of all extant cycads (Fig. 3.3, 3.4) is monosulcate. Comparison of *A. santuccii* pollen in Fig. 2.8, 2.9 with *Cycas revoluta* pollen in Fig. 3.3, 3.4 shows

the close similarity, with smooth proximal and sculptured distal faces in both.

Cycads previously described in the Triassic Chinle flora comprise only 8 species of assorted stems, foliage leaves and scale leaves (Ash, 1985, 1991, 2001). The leaves of *Nilssonia lewisii* Ash (2001) and *Pseudoctenis stewartii* Ash (2001) have stomata similar to those of *A. santuccii*, with simple, narrow, exposed guard cells, and undistinguished subsidiary cells. In having a prominent raised ring of subsidiary cells, the stoma of *Aricycas paulae* Ash (1991, p. 128, fig. 15) are not at all similar to *Androcycas* stoma, but they are, however, similar to the ambiguous rings of cells shown here in Fig. 4.5, 4.6. Two types of un-branched trichomes are present on the leaf of *P. stewartii*, with a short, sac-like type being considerably more numerous than other long narrow hairs (Ash, 2001, p. 20, figs 22, 25.). However, given the indifferent preservation of all the cuticles in question it is not yet possible to suggest which, if any, of the known leaf species *A. santucci* might belong to.

DISCUSSION

We are confident of the cycadalean attribution of this specimen, with strong evidence from extant cycads reinforcing our placing of the specimen in the order Cycadales. However, we are aware that we have not proved beyond doubt that it is male rather than part of a female sporophyll of *Cycas*-type. Because it has not been possible to produce indisputable evidence of *in situ* pollen sacs or their contents, the possibility that the pollen was introduced has to be considered. We have more or less discounted the possibility of the numerous pollen grains having been deposited by wind because they are clearly attached to an inner tissue of the sporophyll (Fig. 2.2). It is unlikely that this was accessible in life and was almost certainly exposed as a result of acid treatment. Insect activity is a stronger possibility as all modern cycads are now known to be insect pollinated (Norstog and Nicholls, 1997, p. 147), by beetles in particular. Because the type of cuticle in Fig. 5 is to be found, as tiny fragments, in almost all the macerations, our assertion that it derives from a vast number of pollen-sacs widespread around the sporophyll seems to us strengthened. Beetle elytra are known from the Chinle Formation and evidence for beetle, and other arthropod, herbivory has been described from several Chinle plant species (Ash, 1997, 1999) and also from coprolites (Ash, 2000). Indeed, insect pollination of cycads must have been well established by the Triassic. Thus it seems most likely that the mature pollen grains on the sample in Fig. 2.1 point to a pollen-filled sac disrupted by feeding insects, rather than deposition by insects visiting a female cone.

Studies relating to the probable Paleozoic pteridosperm ancestry and origin of cycads abound (e.g. Mamay, 1969, 1976; Delevoryas, 1982; Gao and Thomas, 1989; Leary, 1990), almost entirely based on evidence from ovule-bearing structures. Pant (1987) has presented a comprehensive, illustrated review of all the evidence and stated that the "absence of intermediate types of male fructification between the two groups [pteridosperms and cycads] is another difficulty but this may not pose any serious problem since the microsporophyll of the cycads are admittedly homologous to their megasporophylls. Our main difficulty lies in the transitional synthetic forms which can be regarded as ancestral". *Androcycas santuccii* seems to be just such an intermediate type that Pant was anticipating.

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